Increasing CO_2 and plant-plant interactions: effects on natural vegetation

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Abstract

Plant species and functional groups of species show marked differences in photosynthesis and growth in relation to rising atmospheric CO_2 concentrations through the range of the 30 % increase of the recent past and the 100 % increase since the last glaciation. A large shift was found in the compositional mix of 26 species of C_3's and 17 species of C_4's grown from a native soil seed bank in a competitive mode along a CO_2 gradient that approximated the CO_2 increase of the past 150 years and before. The biomass of C_3's increased from near zero to 50 % of the total while that of the C_4's was reduced 25 % as CO_2 levels approached current ambient. The proposition that acclimation to rising CO_2 will largely negate the fertilization effect of higher CO_2 levels on C_3's is not supported. No signs of photosynthetic acclimation were evident for *Avena sativa*, *Prosopis glandulosa*, and *Schizachyrium scoparium* plants grown in subambient CO_2. The effects of changing CO_2 levels on vegetation since the last glaciation are thought to have been at least as great, if not greater, than those which should be expected for a doubling of current CO_2 levels. Atmospheric CO_2 concentrations below 200 ppm are thought to have been instrumental in the rise of the C_4 grasslands of North America and other extensive C_4 grasslands and savannas of the world. Dramatic invasion of these areas by woody C_3 species are accompanying the historical increase in atmospheric CO_2 concentration now in progress.

Introduction

A key global change issue is: does increasing atmospheric CO_2 act directly as a driving force in determining the species composition and physical structure of the earth's vegetation? If so, how does the magnitude of this effect compare with other factors, particularly changing climate? Through the process of plant photosynthesis, inorganic carbon from the atmosphere is incorporated into the biotic component of the biosphere where it plays a commanding role in the mass and energy exchanges of all biological processes including those that ultimately determine the physical structure, species composition and functional development of the earth's ecosystems. The current concentration of CO_2 in the air (ca 350 moles mole^{-1} or ppm) limits photosynthesis of most plants (Lemon 1983), even though the atmospheric level has increased around 30 % over the last 200 years (from 270 ppm; Neftel *et al.* 1985) and has essentially doubled since the last glaciation (from 170 ppm; Delmas *et al.* 1980). Given the current rate of increase, CO_2 is projected to reach 600 ppm by the middle of the next century (Trabalka *et al.* 1985).

It has been hypothesized that elevated CO_2 levels expected in the future will enhance carbon assimilation, water use efficiency and productivity of some species more than others (Osmond *et*

al. 1980) and will modify the general growth responses as expressed in morphology and phenology (Bazzaz 1990). Combined, these altered processes may change the productivity, structure and species composition of naturally occurring vegetation (Overdieck & Reining 1986, Patterson & Flint 1990). These projections are based primarily on evaluations of experimental results from short term CO_2 enrichment experiments which show that species differ markedly in their photosynthetic and growth responses to CO_2. The hypothesis assumes that as global CO_2 levels rise, those species favored most by increased CO_2 will become more competitive and increase in importance relative to those favored least.

A counter-hypothesis advanced by Kramer (1981) argues that increases in photosynthesis in relation to elevated CO_2 are often only temporary, being most pronounced in seedlings or initial stages of growth, and will not greatly affect ecosystem function and productivity. The loss of the capacity to respond to elevated CO_2 has been termed 'CO_2 acclimation' and is viewed as a major unknown in the CO_2 equation for future environments (Bazzaz 1990). One explanation for the rapid loss of sensitivity to higher CO_2 is that other necessary growth resources, such as water, nutrients or light, are more limiting than CO_2 itself in regulating overall carbon gain and the growth process. Kramer (1981) concludes that 'In nature the rate of photosynthesis and biomass production probably is limited more often by water and nitrogen deficiency than by the low CO_2 concentration of the air.'

Evidence for the correctness or deficiencies of either the ecosystem 'stimulation' or the ecosystem 'acclimation' hypotheses should already be recorded in the earth's vegetational record. Global scale experiments in this regard have been performed and replicated by the marked changes in CO_2 levels that have occurred in both the recent and distant pasts (Barnola *et al.* 1987). Any adjustments to changes in CO_2 that have occurred should be represented in the structure and composition of existing vegetation. Information pertaining to questions of how CO_2 affects plant processes should be preserved in the physiology of individual species and reflected in the species composition of plant communities. While reconstructions of vegetational histories from paleoecological records are feasible, our emphasis is on comparing the responses of different kinds of plants growing together today.

Given the hundreds of thousands of plant species presently on the earth, the task of determining their individual CO_2 responses is overwhelming. It is therefore not only convenient but perhaps necessary to simplify the matter by combining plants with similar CO_2 assimilation characteristics into groups. Ideally such classifications can be based on surrogate criteria related to structural, taxonomic and/or functional classifications already established. Such classifications may ultimately provide a mechanistic basis for postulating vegetational differences between a CO_2-enriched and a CO_2-poor world.

An obvious starting point is to evaluate the vegetational consequences of changing CO_2 levels on plant communities made up of C_3 and C_4 plants, which are distinguished by anatomical and biochemical differences in the CO_2 uptake pathway. As a group, the C_4's have an average photosynthetic rate around 50 % higher than the C_3's (Osmond *et al.* 1982). In terms of carbon uptake in photosynthesis and growth, C_4 plants have been categorized as 'efficient' in contrast to 'non-efficient' C_3's (Black *et al.* 1969). However, photosynthetic rates of C_3's show the greatest sensitivity to changing CO_2 levels (Pearcy & Bjorkman 1983). Differences in photosynthesis and growth between C_3 and C_4 species in relation to elevated CO_2 have been the focus of several experiments (Patterson & Flint 1980, Carlson & Bazzaz 1980, Carter & Peterson 1983, Zangerl & Bazzaz 1984, Wray & Strain 1986 & 1987, Curtis *et al.* 1989 & 1990). The working hypothesis has been that increasing CO_2 levels should favor C_3 species by shifting any competitive balance in their direction. Experimental results have generally supported this hypothesis (Patterson & Flint 1990, Long & Hutchin 1991).

This report critically examines the propositions that changing CO_2 levels influence the structure, composition and productivity of vegetation, and

that the changes in CO_2 levels that occurred during the recent (200 years BP) and distant (15,000 years BP) pasts elicited observable changes in vegetation. The specific questions posed are how has the 30 % historical rise in CO_2 and the 100 % rise that has occurred since the last ice age affected vegetation, and further, can understanding this result help in projecting the future biospheric effects of the rapidly accelerating atmospheric CO_2 increase?

Our approach to testing the proposition that atmospheric CO_2 serves as a factor in determining vegetation structure and composition will be to present some of our own observations on species responses to subambient CO_2 levels and to compare these results with other available studies, most of which report responses to superambient CO_2 levels projected for the future. We emphasize a retrospective approach because photosynthesis exhibits the greatest sensitivity to changes in CO_2 below rather than above current levels (350 ppm). The perspective we present on plant-plant interactions is not focused on mechanistic processes but rather on the observed establishment of different population mixes along a CO_2 gradient, followed by a consideration of some of the processes involved in establishing this mix, and some possible implications of the results.

Materials and methods

An experimental growth chamber ('tunnel') was constructed for growing plants across a gradient of subambient CO_2 concentrations for the purpose of looking back in time to see how plants grew at the reduced CO_2 levels of the past. Carbon dioxide levels along the gradient ranged from around 350 ppm (current ambient) through levels indicative of 150 years ago (270 ppm) to below ice age levels (170 ppm) (Delmas et al. 1980).

The tunnel is approximately 39 m long and 0.45 m wide. It is housed in a naturally lighted glasshouse and is configured in a serpentine manner with five sections, each about 8 m in length. Each section is comprised of a narrow soil container (8 m × 0.45 m × 0.7 m) with a volume of about 2500

liters. Attached to the top of the soil container is an inflated, semicircular, transparent polyethylene canopy. The polyethylene canopy used in these experiments had a perimeter of 1.5 m with a center height of about 0.6 m. Light intensity under the canopy is approximately 60 % of that measured on the roof of the glasshouse. Plants in the chamber were irrigated weekly as needed to maintain the water content of the soils near field capacity. The weekly water requirement was determined by monitoring the soil water content with a calibrated surface neutron meter applied to the outside wall of each soil container.

The CO_2 gradient is created by the photosynthesis of plants established along the tunnel. Air forced through the tunnel by a motorized blower is progressively depleted of CO_2 by the plants as it travels down the tunnel. The degree of depletion is determined by the rate of air movement down the tunnel and the photosynthetic capacity of the system. The desired gradient is maintained by varying the rate of air flow (blower speed) in relation to changes in the system's photosynthetic rate. The rate of photosynthetic CO_2 depletion changes in time with shifting environmental parameters (particularly variations in light intensity relative to cloudiness and sun angle) and stage of plant development (particularly photosynthetic surface area). The gradient is maintained during the daylight period by regulating blower speed with feedback signals from a CO_2 infrared gas analyzer measuring the CO_2 concentration of air samples drawn from the end of the tunnel at 2 minute intervals, and a photon flux sensor mounted on the roof that constantly monitors light conditions. Empirical algorithms involving light and CO_2 signals regulate the blower speed. Carbon dioxide measurements at six points along the tunnel indicate the constancy and linearity of the gradient. At night when environmental energy exchange conditions are more benign and less variable the tunnel is ventilated at a constant blower speed to minimize the reversed CO_2 gradient caused by respiration.

Air temperature and air humidity levels are reset to tunnel entrance conditions at the beginning of each 8 m section. The control is mediated

by chilled-water cooling coils and electrical resistance heaters mounted between the five tunnel sections. Feedback signals from humidity and temperature sensors appropriately located in the tunnel evoke heating and/or cooling so as to condition the air passing down the tunnel in accordance with measured values for incoming entrance air. A fuller description of the tunnel system and its specifications for operation and control with regard to CO_2, water vapor, air temperature, soil moisture, etc., is in preparation.

In the first experiment the soil containers were filled with an unsterilized fine sandy loam topsoil from a local savanna occupied by native vegetation. It contained seeds of plant species indigenous to the savanna site where it was obtained. Seedlings from this seed bank were allowed to grow and develop as they would along the CO_2 gradient from early June to early September 1988. Above-ground plant material was then harvested, dried, weighed, and identified with reference to position in the CO_2 gradient. Species were classified according to C_3 or C_4 photosynthetic mode based on literature references, taxonomic affinities and Kranz anatomy. During the course of the experiment the plants interacted freely and competed for water, nutrients, and light.

The second experiment is similar to the first in that it was conducted in essentially the same tunnel system and considers many of the same species but differs from it in both the initial intent and the detailed approach. *Avena sativa* (cereal oats) and one of its weeds, *Brassica kaber* (field mustard) were planted in a classical de Wit replacement design. A separate full report on the results for oats and mustard has been prepared for presentation elsewhere. We consider here the development of other 'weed' species that were permitted to grow during the final weeks of the oats and mustard study. For this experiment, the soil containers were partitioned into increments of 0.6 m to provide a linear sequence of 64 compartments over the entire length of the tunnel. The compartments were filled with remixed soil from the previous experiment. Each soil compartment had a volume of approximately 200 liters. During the first 10 weeks 'weeds' were routinely removed

from the oats and mustard plantings but during the last few weeks of the 15 week growth period the 'weeds' were left to develop. When the oats and mustard were harvested, the 'weeds' were inventoried as to their location along the gradient, and as far as possible, their taxonomic identity. Taxa from the inventory were categorized as C_3 or C_4 species.

An assessment of acclimation to subambient CO_2 concentrations was made for three species, two C_3's, *Avena sativa* (oats) and *Prosopis glandulosa* (mesquite), and one C_4, *Schizachyrium scoparium* (little bluestem), grown in the CO_2 gradient. The latter two species were grown together in an experiment subsequent to those already described. Instantaneous measurements of photosynthetic capacity, as a function of CO_2 concentration, were made on leaves of individual plants grown for several weeks at different positions in the CO_2 gradient. These measurements indicated whether or not acclimation to different CO_2 levels had occurred. A portable ADC gas exchange system was used for the leaf measurements.

Results

Prosopis glandulosa (mesquite), a C_3 small tree, and *Schizachyrium scoparium* (little bluestem), a C_4 perennial grass, differ markedly in their CO_2 assimilation rates in relation to CO_2 concentration (Fig. 1). The C_3 species has a photosynthetic rate lower than that of the C_4 at CO_2 levels below 350 ppm but exceeds the C_4 at concentrations above 350 ppm. The differences illustrated are typical of those commonly reported for C_3 and C_4 types. The point for emphasis in Figure 1 is the striking change in the rate of divergence between the C_3/C_4 and the C_4/C_3 photosynthetic ratios as the CO_2 level drops below current ambient toward the compensation point of the C_3 species, approximately 70 ppm (Fig. 1c). Deflection changes in the two curves graphically illustrate the nonlinearity and magnification of the differences in the relative photosynthetic rates of the C_3 and C_4 types as the atmospheric CO_2 decreases through levels of the recent past.
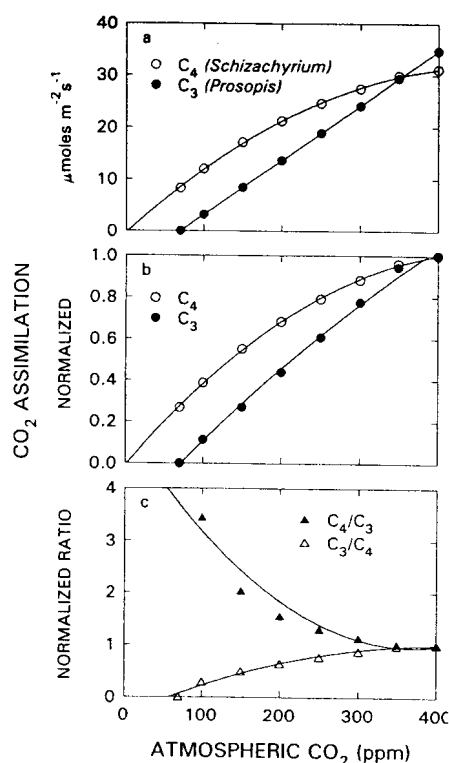
Fig. 1. Photosynthesis as a function of atmospheric CO_2 concentration for *Prosopis glandulosa* (C_3) and *Schizachyrium scoparium* (C_4) under approximately 1400 μmol m^{-2} s^{-1} sunlight; absolute rates (a), rates normalized to the maximum rate observed (b) and the ratios of the normalized rates of the two species (c).

The natural seed bank of the native soil in the CO_2 tunnel yielded 43 species that developed sufficiently for identification. Of these, 26 belonged to the C_3 photosynthetic type and 17 to the C_4 type. More than half of the combined total of both types (25 species) occurred with such low frequency that no distribution pattern, increasing or decreasing, could be discerned along the CO_2 gradient. However, 18 species, 9 C_4's and 9 C_3's, were abundant enough to be subjectively scored as to their distribution pattern along the gradient (Table 1). The overall trend was clearly for C_3 species to increase and C_4's to decrease with rising CO_2, but differences in the degree of response among species in both groups are apparent. In the case of the C_4's, populations of *Cenchrus incertus* and *Paspalum setaceum* showed a strong preference for the low CO_2 end of the gradient while

Table 1. Major plant species grown from a savanna soil seed bank in a CO_2 gradient (150–350 ppm) grouped by photosynthetic mode (C_3 and C_4) and subjectively rated for abundance (scale 1 to 5) and response to increasing subambient CO_2 (+ increased, 0 no apparent trend, − decreased).

Species	Abundance	CO_2 response
C_4		
Cenchrus incertus	5	− − −
Paspalum setaceum	5	− − −
Panicum cappillare	4	− −
Digitaria ciliaris	3	− − −
Eragrostis spectabilis	3	− −
Cyperus globulosus	4	− −
Mollugo verticillata*	4	− −
Sporobolus neglectus	1	−
Euphorbia prostrata	2	0
C_3		
Croton glandulosa	3	+ + +
Verbena hastata	3	+ + +
Rudbeckia hirta	2	+ +
Commelina erecta	2	+ +
Panicum angustifolium	3	+ +
Croton capitatum	2	+ +
Monarda punctata	1	+
Croton monanthogynus	1	+
Oxalis dillenii	3	0

* Often considered a C_3/C_4 intermediate.

Euphorbia prostrata showed no preference. Conversely, the C_3's *Croton glandulosa* and *Verbena hastata* exhibited a strong preference for the high CO_2 end of the gradient while *Oxalis dillenii* showed no preference.

Species judged too sparse for distributional considerations, but included in the combined functional group biomass were: *Amaranthus albus*, *Amaranthus berlandieri*, *Aristida* sp., *Cynodon dactylon*, *Eragrostis secundiflorus*, *Leptoloma cognatum*, *Panicum diffusum*, *Paspalum langei* (the C_4's) and *Diodia teres*, *Euphorbia dentata*, *Gaura* sp., *Gutierrezia dracunculoides*, *Hedyotis rosea*, *Monarda citriodora*, *Monarda fistulosa*, *Oenothera laciniata*, *Parthenium hysterophorus*, *Plantago* sp., *Psoralea* sp., *Smilax* sp., *Solanum rostratum*, *Verbena bipinnatifida* (the C_3's) and three other C_3 types that remained unidentified. Plant nomenclature follows Correll & Johnston (1979).

The biomass distribution of the collective C_3

and C_4 types demonstrated very strong and opposite responses to the CO_2 gradient (Fig. 2). The C_4's, particularly the grasses, exhibited high productivity even at CO_2 levels below 200 ppm. The combined productivity of the C_3 species was much lower than the C_4's, even though more species were involved. The productivity of the C_3's approached zero at CO_2 levels below 200 ppm. The reciprocating responses of the C_3's and C_4's along the CO_2 gradient nearly offset each other. Total biomass of the C_3 and the C_4 groups combined was relatively uniform across the CO_2 gradient (Fig. 3). The smallness of this combined biomass increase is somewhat surprising and can be attributed to a sustained or increased productivity of C_4's as competition from the C_3's diminished with the reduction of the CO_2 concentration. Obvious changes in the proportions of sunlight intercepted by the C_3's and C_4's also occurred as the C_3's became shaded by the larger C_4's at the low CO_2 end of the tunnel and suggested that C_4's are superior competitors for light at low CO_2.

Species listed in Table 1 as well as all the minor taxa listed above contributed to the biomass results (Figs. 2 and 3). Most of the species representing both photosynthetic modes were annuals. Grasses dominated the C_4 component and were only represented in the C_3 group by *Panicum angustifolium*. The experiment took place during
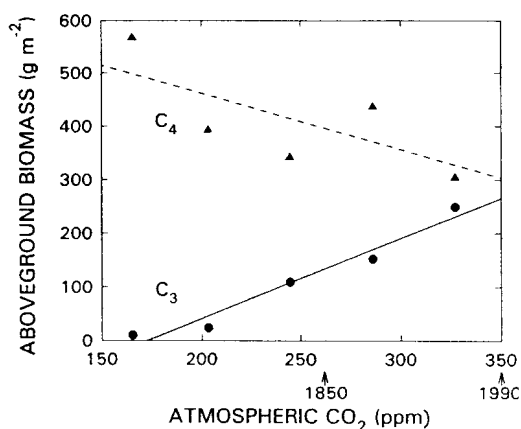

Fig. 3. Total above-ground biomass of C_3 plus C_4 species that developed from a seed bank of a Texas savanna soil over a subambient CO_2 concentration gradient from 150 to 350 ppm over a period of 13 weeks.

summer (June – September) and most of the C_3's as well as the C_4's that contributed substantively to biomass have warm-season growth phenologies (Gould 1975).

In the second tunnel experiment, large increases in biomass of individual plants of the oats and mustard, the two principal species (both C_3's) were again observed as the CO_2 level increased along the gradient (Fig. 4). These marked increases are of the same direction and magnitude as those observed for C_3 species that developed from the native soil seed bank in the first experiment (Fig. 2). Increasing CO_2 by 200 ppm, over the range from 150 ppm to 350 ppm, more than

Fig. 2. Above-ground biomass of C_3 and C_4 species that developed from the seed bank of a Texas savanna soil over a subambient CO_2 concentration gradient from 150 to 350 ppm over a period of 13 weeks.
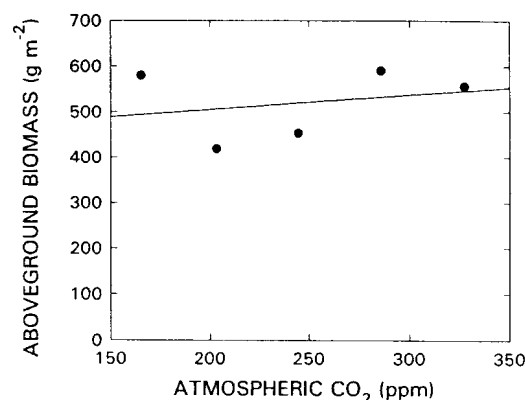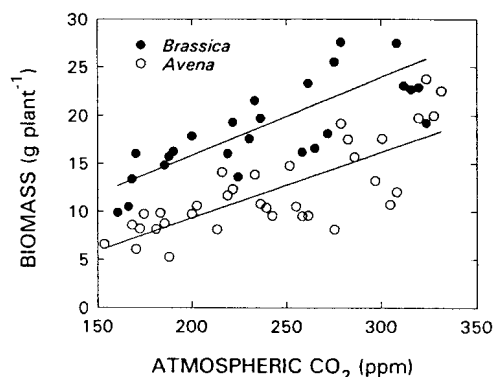

Fig. 4. Above-ground biomass of individual *Avena sativa* and *Brassica kaber* plants grown in a subambient CO_2 concentration gradient from 150 to 350 ppm for 15 weeks.

doubled biomass production of the C_3 component.

Observations on the major C_4 and C_3 weeds that developed during the final stages of the oat and mustard experiment provide additional corroboration of contrasting responses between the two types (Table 2). In the case of the 11 C_4 weed species, a pronounced pattern of increasing frequency with decreasing CO_2 similar to the biomass trend from the first experiment is clearly evident (Fig. 5). Although 19 species of C_3's occurred, their development was meager in comparison to the planted oats and mustard and together they contributed little to the marked increase in C_3 biomass with the increase in CO_2. No consistent pattern in the population distribution of the additional C_3 species could be discerned along the tunnel (Table 2).

The photosynthetic capacity of two C_3's, *Avena sativa* and *Prosopis glandulosa*, and one C_4, *Schizachyrium scoparium*, grown at different CO_2 concentrations in the tunnel for several weeks showed no change in relation to the CO_2 growth level (Fig. 6). Leaves of the individual species selected from the CO_2 levels specified in the figure have nearly identical CO_2 assimilation rates in
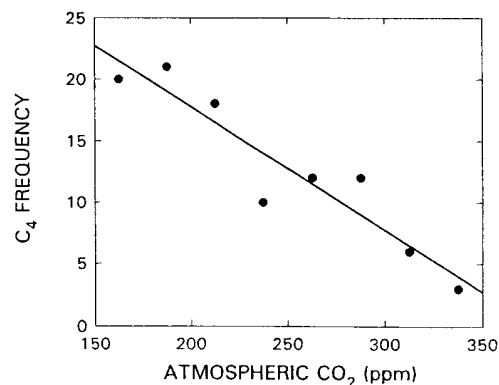

Fig. 5. Frequency of C_4 weeds that developed during the last 5 weeks of a C_3 dominated (*Avena sativa* and *Brassica kaber*) experiment. Frequency data represent the number of occurrences of C_4 species in eight sections of consecutive 0.6 m segments along a subambient CO_2 concentration gradient from 150 to 350 ppm.

relation to a range of short term CO_2 exposure concentrations. Photosynthetic acclimation to rising CO_2 from preindustrial levels to those of the present is not apparent. CO_2 assimilation rates for plants grown at extremes of the CO_2 gradient are essentially the same across both the CO_2 concentration of the air and CO_2 concentration cal-

Table 2. Principal 'weeds' that developed in the final 5 weeks of an *Avena* and *Brassica* CO_2 gradient (150 - 350 ppm) experiment, grouped by photosynthetic mode (C_3 and C_4) and subjectively rated for response to increasing subambient CO_2 (+ increased, 0 no apparent trend, - decreased).

| C_4	CO_2 response	C_3	CO_2 response
Cenchrus incertus	– – –	*Croton glandulosa*	0
Panicum spp.	– –	*Verbena halei*	0
Digitaria ciliaris	– –	*Panicum angustifolium*	0
Cyperus globulosus	–	*Oxalis dillenii*	0
Paspalum setaceum	–	*Commelina erecta*	–
Amaranthus spp.	–	*Oenothera* spp.	0
Eragrostis spectabilis	0	*Ratibida columnaris*	–
Echinochloa crusgalli	0	*Ambrosia artemisiifolia*	+
Setaria sp.	0	*Lesquerella* sp.	0
		Rudbeckia hirta	0
		Gaillardia pulchella	0
		Gaura sp.	0
		Monarda sp.	0
		Plantago sp.	0
		Solanum sp.	0
		Gutierrezia dracunculoides	0
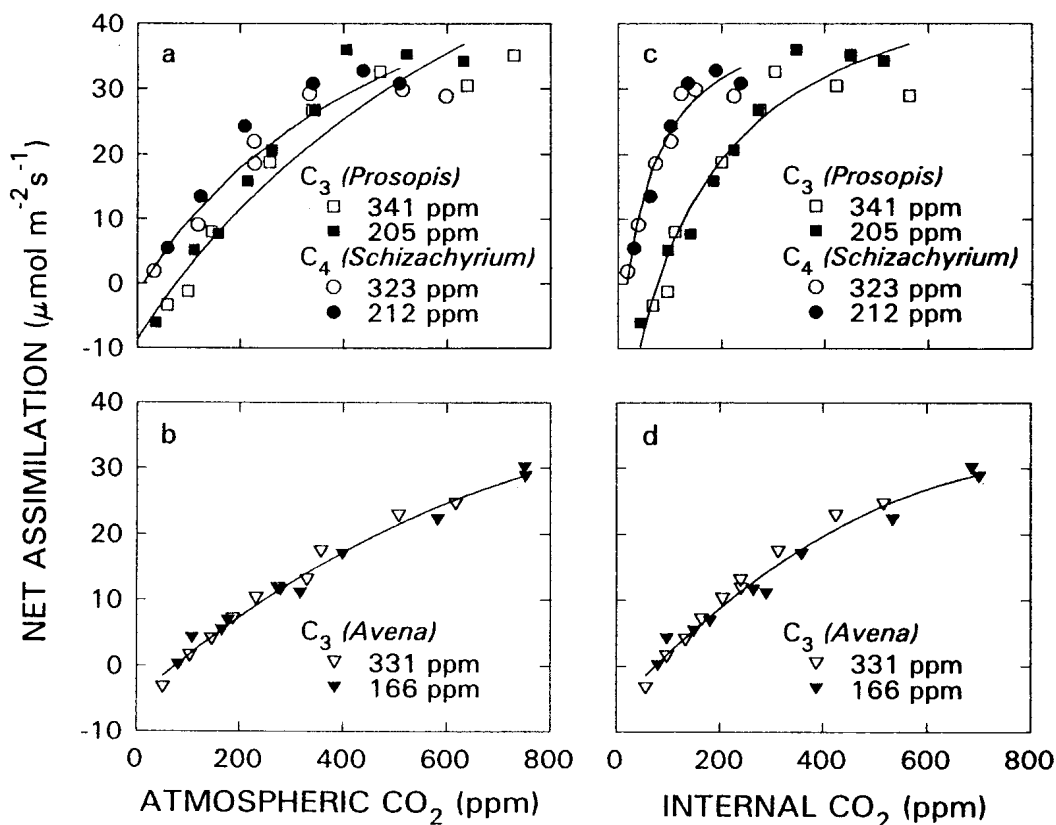
Fig. 6. Instantaneous CO_2 assimilation rates for leaves of Schizachyrium scoparium (C_4), Prosopis glandulosa (C_3) and Avena sativa (C_3) as a function of CO_2 concentration in the atmosphere (a & b) and inside the leaf (c & d) for individual plants of each species grown at the specified CO_2 concentrations.

culated for inside the leaf, indicating the absence of acclimation at both the whole leaf and biochemical levels of organization.

Discussion and conclusions

Comparison of hypotheses

Our results support the hypothesis that changing CO_2 concentration contributes in a major way to the determination of vegetation structure, species composition and productivity. The magnitude of plant response to changes in CO_2 levels per increment of CO_2 rise are much larger at CO_2 levels below current ambient than those reported in the literature for above current ambient. For example, increasing CO_2 by 150 ppm (200 ppm to 350 ppm) doubled the biomass of oats and mustard (Fig. 4) while increases of over 300 ppm above

the current ambient levels are generally reported to increase the biomass of C_3 crops on the order of only 30 % (Kimball 1983). This heightened sensitivity of C_3 species to subambient CO_2 is well illustrated in studies of soybean (Allen et al. 1991) and rice (Baker et al. 1990) in which biomass increase per ppm CO_2 increase was two to three times greater through the subambient range than through current or projected future CO_2 levels. Increasing CO_2 levels in the subambient range elicited a strong growth response for a number of other C_3 species growing in competition with C_4 species (Table 1). Conversely, the C_4's growing with C_3 competition increased their productivity as the CO_2 concentration decreased. This is as expected from differences in the basic photosynthetic response curves of C_3 and C_4 species to CO_2. These curves suggest that the effects of changing CO_2 levels on growth and develop-

ment of C_3 and C_4 species should be neither parallel nor synchronous (Fig. 1).

Our results do not indicate acclimation of photosynthesis to the subambient CO_2 levels experienced in the CO_2 gradient tunnel (Fig. 6) and thus fail to support the acclimation hypothesis that changing CO_2 levels will have little effect on interacting plant populations. Furthermore, even though most reports on CO_2 acclimation suggest that elevated CO_2 causes a reduction in photosynthetic capacity, or 'down regulation' (Kramer 1981, Bazzaz 1990), some show an enhancement of photosynthetic capacity, 'up regulation' (Campbell et al. 1988, Sage et al. 1989). While it is not clear that the extent of the 'down regulation' or the 'up regulation' has always been sufficiently distinguished from phenological state and environmental conditions, particularly pot size effects, it is clear that species differ widely in how they respond to increasing CO_2. Such response differences should serve as a driving force for change in vegetation with changing CO_2 rather than a conserving force for maintaining the status quo.

Carbon dioxide and physiological processes

Although the sensitivity of photosynthesis to CO_2 concentration is a central focus, it is significant that this sensitivity appears to be shared with other interrelated physiological processes such as photorespiration (Pearcy & Bjorkman 1983, Sharkey 1988), quantum yield (Ehleringer & Pearcy 1983), transpiration (Morison 1985) and dark respiration (Gifford et al. 1985, Bunce 1990, Amthor 1991). The effects of elevated CO_2 on all of these processes appear to be favorable in terms of water use efficiency and carbon balance (Idso 1989a). Photorespiration is perhaps the most significant in the context of our discussion since it has a direct mechanistic involvement with several of the other processes.

The striking differences observed in photosynthesis and growth between C_3's and C_4's are directly connected to the presence of the wasteful process of photorespiration in the former but not in the latter. Elevated CO_2 depresses photorespiration in C_3's by competitively inhibiting the

oxygenation of the primary carboxylating enzyme, ribulose-1,5-biphosphate carboxylase/oxygenase. This inhibition is very sensitive to CO_2 level. Ehleringer et al. (1991) contend that with the projected rise in CO_2, photorespiration in C_3 species will be reduced by half by the middle of the next century and will be essentially eliminated if the CO_2 level reaches 1500 ppm.

Looking back in time, Sharkey (1988) estimates that photorespiration in C_3 plants has been reduced 20 % since 1900, with the rise in CO_2 from 290 ppm to 350 ppm, and over 10 % since 1955. If we use Sharkey's method to extrapolate to ice age CO_2 levels (170 ppm) it appears that photorespiration would have been 100 % higher than that today. This would mean that approximately 70 % of the initial carbon assimilated in photosynthesis would be returned as CO_2 through the photorespiratory system. The limitation this would place on carbon accumulation by C_3 plants is on the order of the magnitude of the decreases in biomass observed in the CO_2 tunnel at comparable CO_2 reductions (Figs. 2 and 3). Such limitations for C_3's but not C_4's have significance in how plants may further interact in the development of terrestrial plant communities.

Plant-plant interactions

Species composition is determined by the selective interplay of biotic and physical factors of the environment acting on the genetic pool of the available plant species. Plant-plant interactions are believed to contribute a highly significant part of the biotic interplay. The possible effects that one plant may have on another cover a broad spectrum of theoretical possibilities, ranging from competition through neutralism to mutualism (Malcolm 1966). The theoretical framework set forth by Malcolm describes ten different categories of biotic interactions (some yet unnamed) that make sense biologically. There appears to be no reason to believe that any of the ten should not be operative in most ecosystems. Nevertheless, the recognition and evaluation of such interactions are fraught with difficulties. Techniques for studying most of them are poorly developed al-

though considerable progress has been made in evaluating competitive interactions.

Tilman (1988) presents some persuasive arguments that plant-plant competition is keyed to the relative effectiveness of species in acquiring required resources from a limited resource base. Grime (1979), on the other hand, emphasizes the importance of variable intrinsic growth rates among species as a primary force for establishing the composition and structure of vegetation. All plant growth resources are not comparable in terms of providing equivalent opportunities for inter- and intra-species competitive interactions even when a resource appears to be limiting as in the case of CO_2. Nonetheless, plant growth rates are clearly limited at today's CO_2 level (Fig. 4).

Atmospheric carbon dioxide and competition

The argument that atmospheric CO_2 serves as a growth limiting resource appears somewhat paradoxical since it is also an example of a resource that is essentially equally and consistently available to all plants at all times, such that the supply may almost be considered infinite. However, the rate at which CO_2 can be supplied to plants is limited because of physical diffusional processes and this is equally true for all plant species in terrestrial communities. We conclude that, in the short term, even during the periods of most rapid photosynthesis, individual plants do not compete with each other for the CO_2 they use. That is, we cannot conceive of a situation for terrestrial ecosystems where the CO_2 supply for one type of plant might be diminished sufficiently by the CO_2 utilization and uptake of another type to make a difference in the usual sense of competition. The composition of the atmosphere is highly conservative as a consequence of its large volume and vigorous mixing dynamics.

Effects of changing CO_2 concentrations on the species composition of vegetation and plant to plant interactions are not mediated through competition for CO_2 per se but depend primarily on how the rate of carbon supply influences individ-

ual growth rates and alters the acquisition and utilization of other required resources. In the case of our multispecies tunnel experiment, differences in the growth rate between the C_3's and C_4's resulted in differences in light interception and can be viewed as a change in the ability to compete for light. An increased carbon supply can be expected to affect species differentially through 1) changes in rates of growth and the timing of phenological development, 2) changes in the proportions and absolute amounts of specific growth resources required for completing life cycles and insuring ecological success, 3) changes in the rates at which scarce essential growth resources can be acquired, and 4) changes in the actual habitat requirements.

The consequences of CO_2 level differentially affecting plant species in their growth rate and in their ability to compete for other resources, and even how much of the other resources they may need, has far reaching consequences in establishing the temporal and spatial characteristics of ecosystems.

Vegetation dynamics

We subscribe to the individualistic concept of plant communities as the most realistic framework currently available for understanding the dynamics of vegetation. That is, plant community composition and structure are determined primarily by the responses of individual species to their immediate environment rather than to higher order community processes, as held by the organismic concept of communities (Graham & Grimm 1990, Johnson & Mayeux in press). As a consequence, we contend that understanding why species or functional groups of species respond differently to increasing CO_2 is a key to understanding how vegetation has been or will be affected by changing CO_2 levels. The range of CO_2 levels represented in our experiments are similar to those experienced by the earth's vegetation since the last glaciation. Remarkable changes in vegetation with regard to C_3 and C_4 composition occurred during this period and before. It is suggested by Ehleringer et al. (1991) that C_4 plants

were derived polyphyletically from C_3's during periods of depressed atmospheric CO_2 levels approximately 60 million years ago. Smith (1976) made a similar suggestion, emphasizing the effects of increasing atmospheric O_2 for increasing photorespiration as an evolutionary force in the development of C_4's. We suggest that the development of the CO_2 concentrating system of C_4's in response to negative effects of photorespiration would also have resulted in a predisposition of C_4 plants for improved water use efficiency and the promotion of greater success in water stressed environments. Changes in water use efficiencies in this connection are believed to have exerted profound effects on the development of natural vegetation.

The significance of the linkage between carbon acquisition and water loss in land plants cannot be over emphasized. It is generally accepted that the major barrier plants had to surmount, in moving from aquatic to terrestrial habitats, was the evolution of a morphology and physiology that would permit acquisition of sufficient carbon for growth without being desiccated by excessive evaporative water loss. Water is the master organizer of vegetation, and when atmospheric CO_2 concentrations vary significantly, plant water relations are directly affected, and selective pressures for refinement of the existing evolutionary product should be brought into play (Moore 1989).

Admittedly, differences in absolute rates of photosynthesis do not by themselves dictate vegetation composition and structure. This is evident in present day vegetation. Many species coexist in the same community though they have very different absolute rates of carbon uptake, and the so called non-efficient C_3 plants make up the bulk of the world's vegetation. While our results show strong support for the proposition that, as a group, C_3 plants receive more benefit from increased CO_2 than C_4's (Fig. 2), it is significant to note that at the individual species level pronounced differences in responses occurred within each functional type (Table 1). This suggests that even within the C_4 group some species may benefit from rising CO_2. Patterson & Flint's (1990) sum-

mary of the results of studies on the effects of elevated CO_2 on C_3's and C_4's show that in some instances growth of C_4's is also substantially increased by elevated CO_2 levels.

At subambient CO_2 levels the slopes of photosynthesis-CO_2 response curves of C_4's are often greater, at first, than for C_3's (Fig. 6, Hesketh 1963, Osmond et al. 1980). The slope of the line and the CO_2 concentration at which photosynthesis approaches CO_2 saturation become important considerations in theorizing on the likely effects that changing CO_2 levels may have on C_3-C_4 competition. Conceivably, the sensitivity of photosynthesis and growth of some C_4 species to increasing CO_2 may exceed that of some associated C_3's, particularly in the range of atmospheric levels slightly below current ambient.

The C_4 North American short grass prairie species *Bouteloua gracilis* appears to exhibit a sustained response to rising CO_2 levels to well above current ambient (Reichers & Strain 1988). Such tendencies, along with any attending 'preadaptation' for efficient water use, may have resulted in a superior suitability for certain water stressed habitats not only in the recent past but also, to a more limited extent, in the future. The combined effects of increased carbon assimilation and water use efficiency over the range of CO_2 levels that prevailed until recently would have favored the development of vegetation assemblages with a strong C_4 component. The extensive C_4 grassland known as the North American prairie arose as an identifiable vegetation type since the last glaciation when CO_2 levels dipped to 170 ppm and has become particularly well defined during the last 10,000 years (Wells 1983).

Perhaps more relevant to effects of the historical increase in CO_2 on vegetation is the change in natural vegetation in progress for at least the past 125 years. Grasslands throughout the world are being invaded by C_3 trees and shrubs. Although this phenomenon is popularly ascribed to impacts of modern man, it is now becoming evident that traditional explanations are inadequate to account for all of the changes observed (Mayeux et al. 1991). The spectacular increase in woody C_3 plants that is occurring at the expense

of C_4 grasses is consistent with the responses observed in our experimental system.

Studies on the effects of a doubling of CO_2 on C_3 and C_4 plants in a saltmarsh ecosystem give strong support to the contention that C_3 plants will increase more than C_4's as CO_2 rises (Curtis et al. 1989 & 1990, Ziska et al. 1990). The biomass increase for a C_3 saltmarsh species, *Scirpus olneyi*, is on the order of 30%, about the same as that observed for a doubling of CO_2 in crop plants (Kimball 1983), but is considerably less than we observed for an even smaller CO_2 increase in the subambient range (see also Allen et al. 1991, Baker et al. 1990). This suggests that future gains will be less rapid than those already experienced.

Arctic tundra, with all C_3 plants, is reported to show little response to a doubling of current CO_2 (Oechel & Strain 1985). It has been suggested that the dampened response may be due to low nutrient status (Billings et al. 1984) and/or diminished sensitivity to CO_2 at low temperatures (Idso et al. 1987). But even here, field studies of intact tundra ecosystems indicate significant positive increases in the total annual carbon flux, particularly at the beginning and end of the growing season, when temperatures are relatively low (Hilbert et al. 1987, Grulke et al. 1990). We would suggest that the apparent lack of stimulation to a doubling of CO_2 may be due, in part, to the diminishing response of many plants to increasing CO_2 levels as high as double current ambient, and that greater relative effects may have occurred with the rise from the lower CO_2 levels of the past to those of the present. In other words, a large CO_2 response may already be in process, or almost accomplished, in light of the heightened sensitivity to CO_2 changes in the subambient range. The rise of atmospheric CO_2 from 170 ppm to the present 350 ppm since the last glaciation may be having profound effects on the active vegetation dynamics of tundra-type ecosystems (Neustadt 1984).

We are aware that there is risk in extrapolating our results with mostly short lived herbs to long lived woody perennials which make up the bulk of the established natural vegetation of the world. Nevertheless, the same processes that operate in annuals also operate in perennials and consequently will result in effects expressed at the level of vegetation structure and composition. In fact, it can be argued that the enhanced growth observed in annuals should be magnified temporally and spatially in perennials through 'the compound interest law of plant growth' postulated long ago by Blackman (1919). Such an effect is shown in the results of Idso et al. (1991) for sour orange trees, in which the margin of difference between plants grown at ambient and elevated CO_2 increases annually. The compound interest law of increase for perennials is also evident in the response of water lilies to elevated CO_2 (Idso et al. 1990). Looking back in time, LaMarche et al. (1984) conclude that the widths of growth rings in bristlecone pine have increased in a manner more consistent with the rise in atmospheric CO_2 over the last half century than with any other environmental change.

Implications for climatology

Climate is traditionally considered as the primary determinant of vegetation structure, composition and productivity (Webb 1986, Woodward 1987). The strong differential responses of species to varying CO_2 levels and the marked fluctuations in CO_2 levels that have occurred through glacial periods to the present should give pause to the dogma that natural vegetation serves as a near perfect integrator of climate either today or in the past. It seems highly probable that changing CO_2 levels have had, are having and will continue to have a significant modifying influence on the control that climate exerts on vegetation. This points to the distinct risk inherent in using present day vegetation as an unqualified surrogate for past or present climates, a caution sounded earlier by Idso (1989b). It calls into question the common practice in climatology of using paleoecological information, primarily botanical data, for structuring the presumed synoptic conditions of past and future climates, or vice versa, changes in vegetation based on model predictions of changes in climate (Overpeck et al. 1991).

It seems highly probable that changing CO_2 levels substantially modify the control of climate on vegetation productivity, species composition and physiognomic structure. Changing CO_2 levels should be considered as a contributor to the non-equilibrium history of vegetation that now is being so convincingly documented by paleoecolgical studies throughout the world (Johnson & Mayeux in press). Indeed, the direct effects of changing CO_2 levels on vegetation of the past, present and future should be viewed as a powerful influence operating sometimes simultaneously and sometimes independently of shifting temperature and precipitation regimes.

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